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Nursery-area function of maerl grounds for juvenile queen scallops *Aequipecten opercularis* and other invertebrates

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ABSTRACT: The services provided by coastal ecosystems such as mangrove forests and sea-grass beds are becoming increasingly recognised, yet the functional role of maerl beds has not been addressed. Maerl forms highly biodiverse habitats composed of loose-lying coralline red algae which build up over thousands of years. These carbonate-rich deposits occur in photic areas with strong water movement; they have a widespread global distribution yet remain one of the most overlooked shallow-water marine habitats, with little known about the ecosystem services maerl may provide. Our diving research in Scotland has shown that pristine live maerl (PLM) grounds fulfil nursery area prerequisites for commercial populations of queen scallops *Aequipecten opercularis* and other invertebrates, such as the soft clam *Mya arenaria*, the sea urchins *Psammechinus miliaris* and *Echinus esculentus*, and the starfish *Asterias rubens*, more effectively than impacted dead maerl and other common substrata. The complex architecture of maerl beds attracts high densities of these juvenile invertebrates, which use PLM grounds as nursery areas in preference to adjacent substrata. Considering its global distribution, it is highly likely that ecosystem services provided by maerl are considerable. Maerl is easily damaged and killed by a variety of human activities, yet its protection would maintain vital nursery area function, benefiting commercial fishery yields and, pivotally, regional biodiversity.

KEY WORDS: Maerl habitat · Ecosystem services · Nursery areas · Scallops · Marine invertebrates · Scotland

INTRODUCTION

Maerl is a carbonate-rich type of marine sediment deposited by loose-lying calcified algae (Rhodophyta: Corallinales) (Giraud & Cabioch 1976). It is dredged industrially as a source of soil conditioner (Grall & Hall-Spencer 2003) and subject to international conservation legislation provisions (Donnan & Moore 2003). Maerl deposits build up over thousands of years in areas characterised by strong water movement (tidal and/or wave action) in the photic zone (Grall & Hall-Spencer 2003). Varying in area from 10s to 1000s of m^2, maerl grounds occur from the tropics to polar waters and form a gravel composed of high numbers of usually monospecific thalli (Woelkerling 1988).

These coralline algal gravels support an extremely diverse fauna and flora (BIOMAERL Team 2003, Steller et al. 2003) and have significantly greater structural heterogeneity than common adjacent substrata (Kamenos et al. 2003). This is perhaps to be expected, as high heterogeneity equates to high biodiversity in many marine systems (Purvis & Hector 2000, Tilman 2000, Sala 2001). However, maerl is slow-growing, fragile and easily damaged, and a single impaction event with hydraulic fishing gear and scallop dredges significantly reduces the heterogeneity of maerl thalli by breakage, and kills the thalli by burial (Hall-Spencer & Moore 2000, Hauton et al. 2003, Kamenos et al. 2003), changing a pristine live maerl (PLM) ground into an impacted dead maerl (IDM) ground (Kamenos et al. 2003).

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Whilst the ecosystem services provided by coastal habitats such as mangrove forests (Schiermeier 2002) and sea-grass beds (Naylor et al. 2000) have been increasingly recognised, the services provided by maerl habitats have not been addressed. Rocky habitats dominated by coralline algae (e.g. *Lithophyllum* sp.) are often described as 'coralline barrens' due to their low diversity and low structural heterogeneity (Rowley 1989, Sala et al. 1998). Coralline algal gravels are very different, forming structurally complex sediments noted for their high biodiversity of juvenile invertebrates (BIOMAERL Team 2003). We focus herein on the commercially important queen scallop *Aequipecten opercularis*, drawing attention to the economic importance of the PLM habitat, as the importance of benthic habitats is becoming central in fisheries management (Kaiser et al. 2002). We also provide data on the nursery area function of maerl for other marine invertebrates, with observations on sea urchin *Psammecinus miliaris*, *Echinus esculentus* starfish *Asterias rubens* and clam *Mya arenaria* population densities during their most elusive period, i.e. after settlement and before recruitment to adult populations.

Although scallop settlement has been well studied (Eggleston 1962, Le Pennec 1974, Minchin 1981, Pawlik 1992, Harvey et al. 1995, 1997), there are few observations after detachment from primary settlement surfaces but prior to colonization of adult habitats. Some species move little, such as the bay scallop *Argopecten irradians* which uses sea-grass beds both as a nursery area and an adult habitat (Arnold et al. 1998, Bologna & Heck 1999, Irlandi et al. 1999), whereas commercial NE Atlantic scallops are more mobile. Juvenile queen *Aequipecten opercularis* and great *Pecten maximus* scallops attach primarily to various algae, including *Laminaria saccharina* and *Desmarestia aculeata*, but also to bryozoans, hydroids, gravel, clean shell and general benthic epifauna (Eggleston 1962, Paul 1981, Minchin 1992); but we know little about how they subsequently recruit onto adult habitats.

In this study we were interested in the intermediate role played by maerl habitats as ecosystem service providers, particularly as coralline algae have a macromolecular fraction of GABA (γ-aminobutyric acid) which chemically stimulates invertebrate settlement (Giraud & Cabioch 1976, Morse et al. 1980, Morse & Morse 1984), for example by gastropods *Haliotis* spp. (Morse & Morse 1984, Daume et al. 1999, Day & Branch 2002) and polychaetes *Spirorbis* spp. (Gee 1965, Crisp 1974). Scallops are known to respond to chemical cues during metamorphosis and settlement (Pawlik 1992, Harvey et al. 1997). In *Pecten maximus* for example, metamorphosis can be induced by jacaranone extracted from the red algae *Delesseria sanguinea* (Yvin et al. 1985, Cochard et al. 1989). Recently, post-settled juvenile queen scallops have been shown to be attracted to live maerl, possibly by the presence of GABA or the biofilm associated with the presence of the live maerl veneer (Kamenos 2004, Kamenos et al. 2004a). In the presence of predators, live maerl with highest heterogeneities was selected preferentially, with juvenile queen scallops using the inter- and intramatrix spaces of maerl thalli as refuges (Kamenos et al. 2004a). Similarly high numbers of juvenile *Placopecten magellanicus* (Brethes & Bourgeois 2003) and *Chlamys islandica* (Himmelman & Guay 2003) have been observed associated with empty scallop shells resting on less heterogeneous substrata. It is predicted that other juvenile invertebrates will also utilise the maerl matrix in a similar manner to scallops.

Despite the global distribution of maerl, it remains one of the most overlooked shallow-water marine habitats. We describe maerl and other substratum usage, focusing on juvenile queen scallops but including other invertebrates on PLM, IDM and comparative substrata on the west coast of Scotland at various spatial and temporal scales.

MATERIALS AND METHODS

Sampling sites. We selected 9 sampling sites on the west coast of Scotland at −3 to −12 m chart datum within the Clyde Sea area, Loch Sween, Loch Carron and Loch Torridon (Fig. 1). At all sites, either PLM or IDM (*Lithothamnion glaciale* and *Phymatolithon calcareum*) was present along with other common comparative substrata. Gravel was present at all sites except Site 2, and was used as a comparative standard for other substrata. All IDM sites were in the Clyde Sea area and have, in the past, been heavily impacted by scallop-dredging (Kamenos et al. 2003), all other sites assessed have suffered no physical anthropogenic impaction and were in pristine condition (assessed using the techniques described by Kamenos et al. 2003).

Sampling regime. Site 7 was surveyed every 2 mo from February 2002 to February 2003. Other sites (Fig. 1) were surveyed once in winter 2002/2003. Densities of juvenile *Aequipecten opercularis* (<45 mm shell height, sh; for sample numbers see Fig. 3) were quantified using timed SCUBA transects. Randomly selected transects were swum by 2 divers at 9 to 10 m min^{-1} for 5 min. All transects were surveyed at slack water ±2 h to minimise current effects on swimming distance. Scallops observed in a 2 m wide strip were measured and recorded along each 50 m transect (transect area = 100 m^2). Species, time of sighting, shell height and total number of individuals in each transect were recorded. Erect algae were inspected for the at-

Fig. 1. Areas on west coast of Scotland where surveys were completed in winter 2002/2003. 1: Ardlamont Point; 2: Brodick Bay/Merkland Point; 3: Craeg Gobhainn; 4: Stravanan Bay; 5: Tan Buoy; 6: North Strome Slip; 7: Caol Scotnish; 8: Linne Mhuirich; 9: Inner Loch Torridon

tachment of juvenile *A. opercularis* on each sampling trip at Site 7. *Asterias rubens* (<3 cm diam at Site 7), *Echinus esculentus* (<5 cm diam at Site 9) and *Mya arenaria* (siphon < 0.5 cm diam at Site 9) densities were surveyed in randomly selected 20 m^2 transects (n = 5 per substratum) using SCUBA. *Psammechinus miliaris* (<2 cm diam) densities were surveyed using randomly selected 2.5 m^2 quadrats (n = 8 per substratum) by SCUBA at Site 9.

Data analysis. Data were analysed using Minitab® Version 13 and Excel®. Data sets did not deviate significantly from the assumptions required by the associated tests. Juvenile scallop densities at each site/substratum were analysed using multiple-comparison Kruskal-Wallis tests between substrata. Temporal changes in scallop densities at Site 7 were analysed using a repeated-measures ANOVA. Due to the presence of an interaction (substratum and month) post-hoc Tukey pairwise comparisons were carried out using cell and not level means, using the error MS, which is the denominator MS, of the interaction term (Neter et al. 1996). All other species densities were compared using 1-way ANOVAs.

RESULTS

Juvenile queen scallop (<45 mm sh) densities were significantly (H_5 = 94.32, p < 0.0001) (Fig. 2) higher on PLM than on all other substrata surveyed (IDM, gravel, sand, rock, sea-grass) for 9 sites on the west coast of Scotland (Fig. 1).

Surveys every 2 mo over a 14 mo period indicated significantly higher juvenile queen scallop densities on PLM than on gravel or rocky substrata at Site 7 (F_2 = 180.62, p < 0.0001). Juvenile population densities on gravel were significantly higher than those on rocky substrata only during June and August 2002; at all other times no differences were detected (Fig. 3). For all substrata, juvenile queen scallop densities were significantly highest in December (F_6 = 29.04, p < 0.0001) (Fig. 3). During 91 SCUBA dives (136.5 man-hours) at Site 7, only 6 queen scallop juveniles were observed on non-coralline algae: 5 on *Halidrys siliquosa* (growing on rock) and 1 attached to *H. siliquosa* (on PLM). Shell height frequencies of all *Aequipecten opercularis* mea-

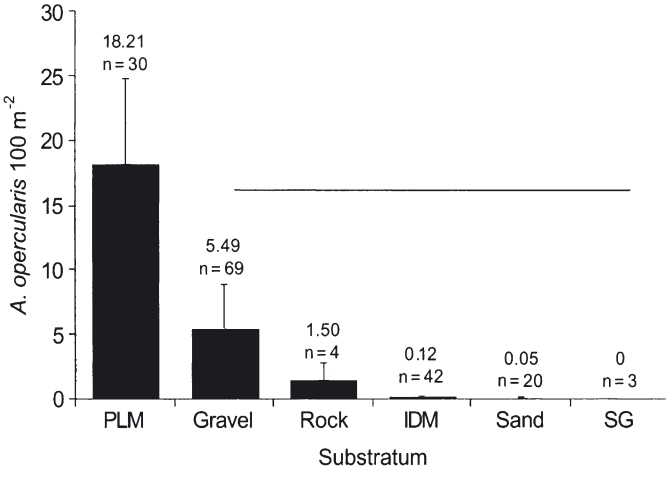

Fig. 2. *Aequipecten opercularis*. Mean juvenile (<45 mm shell height) densities on pristine live maerl (PLM), impacted dead maerl (IDM), gravel, rock, sand and sea-grass (SG) at 9 sites on west coast of Scotland. Error bars = SD; horizontal bar = non-significant (p > 0.05) differences

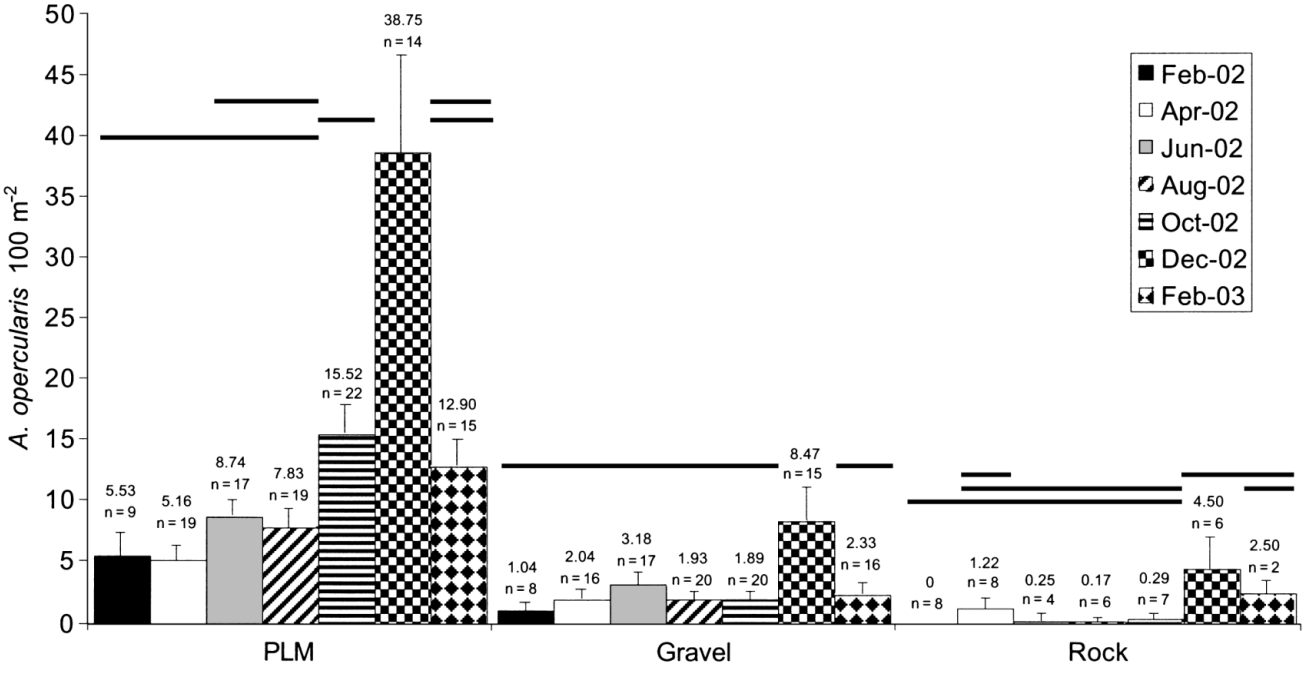

Fig. 3. *Aequipecten opercularis.* Mean juvenile (<45 mm shell height) densities on pristine live maerl (PLM), gravel, and rock substrata during 7 surveys every 2 mo from February 2002 to February 2003 at Site 7 (Caol Scotnish). Error bars = 95% CI. Horizontal bars at same level = non-significant differences ($p > 0.05$)

sured indicated that recruitment to all substrata occurred in October to December. There was a greater increase in scallop densities on PLM in October and December than the corresponding increases observed on gravel and rocky substrata ($F_{12} = 4.6$, $p < 0.0001$) (Fig. 3).

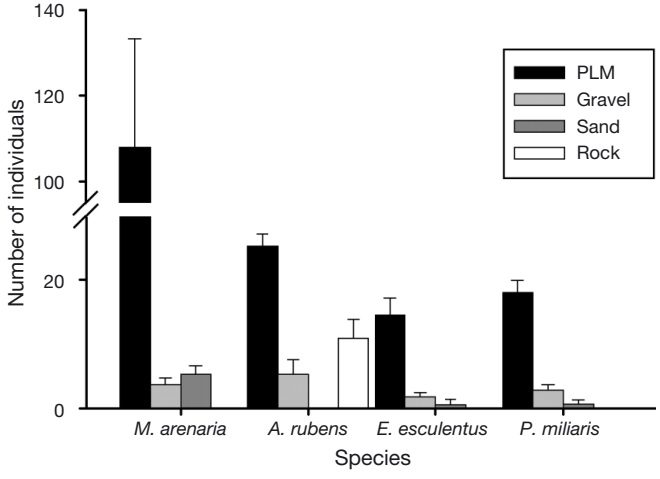

Fig. 4. *Mya arenaria* 20 m^{-2} (n = 5), *Asterias rubens* 20 m^{-2} (n = 5), *Echinus esculentus* 20 m^{-2} (n = 5) and *Psammechinus miliaris* 2.5 m^{-2} (n = 8). Mean numbers of juveniles on pristine live maerl (PLM), gravel, sand and rock on west coast of Scotland. All species were sampled on PLM, gravel and sand, apart from *A. rubens* which was sampled on PLM, gravel and rock

Juvenile *Psammechinus miliars* densities on PLM (18.2 ± 2.7 (mean ± SD)) were significantly higher ($F_2 = 187.17$, $p < 0.0001$) than those on gravel (2.9 ± 1.2) and sand (0.6 ± 0.9) during winter in Loch Torridon. Juvenile *Echinus esculentus* densities on PLM (14.6 ± 3.1) were significantly higher ($F_2 = 57.9$, $p < 0.0001$) than those on gravel (1.8 ± 0.8) and sand (0.6 ± 0.9) during winter in Loch Torridon. Juvenile *Asterias rubens* densities on PLM (25.4 ± 2.1) were significantly higher ($F_2 = 72.5$, $p < 0.0001$) than those on gravel (11 ± 3.4) and sand (5.4 ± 2.5) during winter in Loch Sween. Juvenile *Mya arenaria* densities on PLM (108 ± 28.9) were significantly higher ($F_2 = 221.38$, $p < 0.0001$) than those on gravel (3.8 ± 1.1) and sand (5.4 ± 1.5) during winter in Loch Torridon (all spp.: Fig. 4).

DISCUSSION

We have shown that live maerl grounds provide a critically important service amongst the patchwork of shallow-water NE Atlantic coastal habitats. These structurally complex carbonate sediments consistently harbour significantly higher numbers of juvenile queen scallops and other juvenile invertebrates than adjacent habitats. Parallels can be drawn with the ecosystem services provided by other structurally complex biogenic habitats. Maerl habitats are similar to the

marine habitats formed by kelp forests, sea-grasses and mangroves. In each of these cases, perennial primary producers provide habitats that are essential in the life histories of associated marine life. Juvenile invertebrates utilise maerl habitats in much the same way as juvenile cod utilise kelp forests (Lindholm et al. 1999), juvenile wrasse, bream, cod and scallops utilise sea-grasses (Moore & Jennings 2000) and juvenile prawns and finfish utilise mangroves (Primavera 1998, Naylor et al. 2000), i.e. for the provision of food and shelter from predation (Kamenos 2004).

Juvenile queen and great scallops tend to attach primarily to debris such as clean shells or to erect benthos such as macroalgae, bryozoans and hydroids (Eggleston 1962, Paul 1981, Minchin 1992). Where PLM was present, *Aequipecten opercularis* juveniles were attracted away from the substrata on which they initially settle (Kamenos et al. 2004a). They used PLM to fulfil nursery area prerequisites preferentially to IDM, gravel, sand, and rocky substrata as well as sea-grass, *Halidrys siliquosa*, *Chorda filum* and laminarian algae. Movement of juvenile *A. opercularis* from a settlement substratum to nursery sites may be facilitated by their high surface area-to-volume ratio and thin, light shells. Thus they are easily transported (Minchin 1992), particularly in regions with strong currents such as over maerl grounds. Spat have been observed to use post-metamorphic byssal drifting (Beaumont & Barnes 1992) and are active swimmers, with adult populations shown to migrate large distances (Mathers et al. 1979).

Scallops spawn during August/September in UK and Irish waters (Minchin 1992). This is followed by post-settlement recruitment, with significantly higher population densities of juvenile scallops observed on all substrata during October to December, as we have observed. The reduction in juvenile scallop densities from December to January was probably caused by a combination of predation of new recruits, growth of the older cohort to >45 mm shell height and migration of older juveniles to adult populations.

Juvenile *Aequipecten opercularis* are attracted to PLM by an hierarchical series of chemical and physical cues (Kamenos et al. 2004a) known to occur in other settling invertebrates (Crisp 1984, Chia & Koss 1988), using maerl thalli as a refuge in the presence of predators (Kamenos et al. 2004a). It is likely that the higher post-settlement recruitment to PLM rather than gravel and rock substrata, observed in December at Site 7, is attributable to such stimuli, combined with the refuge capacity of PLM and the subsequent effects that refuge utilisation has on differential predation between PLM gravel and rock substrata.

The significantly higher juvenile queen scallop population densities in February 2003 than in February 2002 may be attributable to (1) delayed recruitment in 2002, thus higher scallop densities at the end of the 2002 recruitment period would still have been present in February 2003, (2) a better recruitment in 2002 than 2001, that would have increased scallop densities in general, (3) improvement in juvenile queen scallop recognition on PLM by the authors and (4) any combination or all of these factors.

This is the first report of live maerl grounds being consistently used by commercially important invertebrates during a critical phase in their life histories, i.e. between settlement and their appearance in adult populations. It is likely that, similar to bay scallops in sea-grass beds (Bologna & Heck 1999), PLM offers the optimum compromise between food supply and refuge availability and thus the highest growth potential for residing juvenile queen scallops and other invertebrates (Kamenos 2004). Although our study focused on the commercially important queen scallop as an indicator of ecosystem service provision, the observation that other juvenile invertebrates were found in significantly higher population densities on live maerl than adjacent substrata indicates the wider importance of PLM in the provision of nursery areas. Not only do juveniles of mobile commercially important (*Aequipecten opercularis* and *Psammechinus miliaris*) and non-commercially important (*Asterias rubens* and *Echinus esculentus*) species utilise maerl grounds, but also a commercial species (*Mya arenaria*) which has a mobile juvenile phase and a sedentary adult phase (Yonge 1949). This is highly significant as it indicates that, while mobile, juvenile *M. arenaria* use PLM grounds to fulfil nursery-area prerequisites, possibly gaining anti-predatory or growth advantages, before recruiting to sandy substrata where the sessile adult populations burrow deeply to avoid predation.

Our study has focused on maerl grounds in Scotland. However, these coralline algal gravels have a widespread global distribution (Foster 2001). A fertile area for future research would be to determine whether maerl beds are just as important for commercial species and juvenile invertebrates at other sites around the globe. In Scotland, not only do PLM grounds fulfil nursery area prerequisites for commercially exploited species, but also the destruction of these fragile habitats will be ecologically and economically detrimental to regional biodiversity.

Understanding the importance of benthic habitats is becoming central in fisheries management, e.g. the concept of 'essential fish-habitat', as we attempt to avoid fish-stock collapses. The high juvenile biodiversity and biomass associated with maerl grounds (BIOMAERL Team 2003), combined with findings of this and other studies (Kamenos 2004, Kamenos et al. 2004a,b), indicate that maerl grounds supply many of the prerequisites of a nursery area, including high

juvenile densities, somatic growth and survival, to a wide array of organisms. Maerl habitat degradation has been noted world-wide (BIOMAERL Team 2003); such losses will diminish nursery-area function and reduce regional biodiversity, and may damage commercial fisheries. Given such findings, more urgency is needed to conserve maerl habitats and the ecological services they provide.

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